Antagonistic Muscle Action During the Initiatory Stages of Voluntary Effort

DOUGLAS J. WILSON

A thesis submitted in conformity with the requirements
for the degree of Doctor of Philosophy in the
Department of Psychology of the
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THESIS

The literature on muscle action contains various views concerning how antagonistic muscles act to produce co-ordinated limb movements. Physiological experiments at the reflex level in chronic spinal and decerebrate animals have established the principle of simple reciprocal innervation, *i.e.*, that the antagonistic relaxes when the protagonist contracts. This conception is widely though not exclusively accepted as characteristic of muscle action in the intact organism.

The present study examined the *initial* action of antagonistic muscles during change from rest to effort on the part of one adult subject using finger movement. Kymographic records were taken of the direction, type and time of initial movement of the finger and of both muscles under four conditions, fixation with loads, pursuit, single strokes, reciprocating strokes.

The results show that both antagonistic muscles are active *contractively*; that the time relation between the muscles is irregular and depends upon both external and internal factors; that the angle of muscular response differs for the two muscles.

It is concluded that the muscle action initiated by an intact human subject in response to prescribed tasks is not that of simple reciprocal innervation; instead, both muscles contract either simultaneously or in succession but at different rates and amounts. In terms of effector action this is termed double reciprocal innervation.

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I. Historical Introduction

This research investigates the type of activity that is characteristic of antagonistic muscles in man during voluntary effort. It concerns the question of how co-ordinated motor adjustment is effected. A brief historical review of studies leading up to the concept of "reciprocal innervation" is included as a background for the precise statement of the problem dealt with in this research.

Historically, the study of co-ordinated movement has been divided by Tilney and Pike (1) into two periods, speculative and experimental.

A. *Speculative Period*

In the former period three views regarding the nature of antagonistic muscle action were advanced:

(i) The view advanced by Galen (second century) that when the active muscle contracts the antagonist remains "passive" or "dormant";

(ii) The view of Descartes (seventeenth century) that when the active muscle contracts, the antagonist definitely relaxes. The mechanism for this was described by him as peripheral in that vital spirits were transferred from one muscle to the other.

(iii) The view first advanced by Winslow (1732) and upheld by Duchenne of Boulogne (1867) that when the active muscle contracts the antagonist also contracts, but to a lesser degree. Winslow described the opposing antagonists as "moderators." This view of co-contraction is expressed by Duchenne as follows:

> This nervous action causes on the one hand the contractions of the muscles which produce these motions and on the other, the immediate and parallel contractions of the muscles called antagonists which modify and stabilize them. (Quoted by Fulton (2), p. 446.)

From these three views arises an important issue in co-ordinated movement—the problem of what happens to the antagonist during activity of the protagonist, and what movement of the limb results from such action. The first of the above views apparently did not

gain much support, and so speculation centered about the second and third possibilities; these are described by Tilney and Pike as the French and English schools respectively. During the nineteenth century these two views were vigorously debated. Observations made under exact conditions were necessary before the evidence could be found to support either one view or the other. Towards the end of the century such experimental work was carried out.

B. *Experimental Period*

(i) *Physiological Investigations*

The experimental study of co-ordinated movement may conveniently be dated from Sherrington's publication in 1893 of his first Note on the "Knee Jerk and the Correlation of Antagonistic Muscles" (3) in which he indicated that by reflex mechanism the degree of tension in one muscle intimately affected the tonus in the other. This correlation he described in his third Note (1897) with the phrase "Reciprocal Innervation"; in this note he says:

> One muscle of an antagonistic couple . . . is relaxed in accompaniment with active contraction of its mechanical opponent. . . . The observations to be mentioned below do actually extend this kind of reciprocal innervation to the muscles of antagonistic position acting about certain joints of the limbs. (4, p. 414.)

This position, maintained throughout his fourteen "notes," and in his classical monograph, "The Integrative Action of the Central Nervous System" (1906), is that:

> where two muscles would antagonize each other's action, the reflex arc, instead of activating merely one of the two, causes, when it activates one, depression in the other. (5, p. 84.)

Such a reaction he calls a reflex of double sign, meaning that there is a twofold activity, one muscle contracting positively, the other definitely relaxing. This relationship is simultaneous but reversible, *i.e.*, may continue throughout a series of oscillations. In order that one muscle shall relax while the other is activated, it is necessary that some kind of active inhibition take place in the relaxing muscle. This he called "reciprocal inhibition" and maintained that a study of various reflexes of the body "supports the view that reflex inhibition (relaxation), and the reflex excitation (contraction) are part and parcel of one and the same reflex reaction." (5, p. 93.)

In the fourteenth Note, Sherrington (6) described "double reciprocal innervation," which involved the simultaneous stimula-

tion of *two* afferent nerves, each connecting with both antagonists, so that their individual action on these muscles would be opposite in sign. The result of this double stimulation was that both antagonists contracted to some degree, the greater contraction occurring in the muscle whose afferent nerve had received the stronger stimulus. This composite result he described as an ''algebraical summation''; in point of fact this means that both muscles may actually contract simultaneously in proportion to the strength of the positive and negative stimuli they respectively receive. He believes this to represent conditions ''nearer to the occurrences of daily life'' than is the case of simple reflex contraction of a protagonist with relaxation of its antagonist. (7, p. 268–9.)

It is important in discussions that concern reciprocal innervation at various levels of complexity, from a reflex of a spinal preparation to a voluntary act, to note the distinction made by Sherrington between ''simple'' reciprocal innervation, where contraction of the protagonist and co-relaxation of the antagonist is undeniably the rule, and ''double'' reciprocal innervation, where co-contraction is characteristic. The phrase ''reciprocal innervation'' has been accepted in physiological and psychological circles, but its meaning is not always clear nor perhaps consistent. Thus Fulton, in his chapter on *Co-ordination of Antagonistic Muscles*, describes ''double'' reciprocal innervation as reported by Sherrington, but in his definition of reciprocal innervation seems, if we understand him aright, to be describing only the ''simple'' type:

> Reciprocal innervation merely states that *increase* of contraction (or the converse) does not proceed simultaneously in opposed muscles. By this is meant that as contraction progresses in a muscle (*e.g.*, of an extensor), contractile activity diminishes *pari passu* in the antagonistic flexor. (2, p. 447.)

Throughout the chapter, Fulton contrasts ''synchronous co-contraction'' with ''reciprocal innervation,'' restricting the latter term to the simple reflex phenomenon, whereas Sherrington extended it to cover double reciprocal innervation, *i.e.*, the more complex functioning of daily life. In our experiment we shall define the terms simple and double reciprocal innervation in respect of the actual performance of the antagonistic musculature rather than of conditions of neural stimulation which are usually inaccessible in the intact human subject. Thus, *simple* reciprocal innervation is any case where the antagonist relaxes concurrently with contraction of the protagonist, and *double* (or *multiple*) reciprocal innervation is any case where the antagonist either increases in contraction or

remains at a given state of contraction while the protagonist is contracting. Conceivably, either simple or double reciprocal innervation as here used, might be the result of algebraical summation in Sherrington's sense of double innervation as described above.

By stimulating the appropriate portion of the internal capsule rather than an afferent nerve, Sherrington and Hering (8) in 1898 reported the phenomenon of simple reciprocal innervation in antagonistic muscles of an experimental animal. Similarly by stimulating an appropriate motor center for a flexor, the corresponding extensor is simultaneously relaxed. Later experiments by Sherrington revealed that when two cortical centers, functionally antagonistic to one another, are stimulated the resulting action represents double reciprocal innervation or algebraical summation in muscular activity. On the other hand Tilney and Pike (1) using cortical stimulation presumably of a single center controlling the antagonistic system tibialis anticus and gastrocnemius, obtained in the overwhelming majority of cases a co-contraction of the two antagonists. This seems at variance with the simple innervation results quoted from Sherrington. Does it mean that cortical stimulation may give either simple or double reciprocal innervation depending perhaps on the amount of electrical involvement?

Physiological studies, based on spinal reflexes and cortical stimulation have thus indicated two types of reflexive integration of muscle activity, namely, that in which simultaneous contraction and relaxation occurs in antagonists and that giving co-contraction of antagonists. These basic studies, however, which depend on incision methods with animals do not lend themselves to the investigation of voluntary muscle activity with the organism intact and psychologically controlled.

Investigations have also been conducted with human subjects to discover the process of muscle action during voluntary effort. The experimental evidence thus far is not conclusive, some indicating that there is relaxation of antagonists during voluntary movement, some indicating simultaneous co-contraction. An example of the former is offered by Beevor in his Croonian lectures of 1904. He maintained on clinical evidence that during voluntary movements, especially those made against mechanical resistance, the antagonists always relaxed while the protagonists contracted (9). In support of the opposite view, using electro-physical methods, Golla and Hettwer (10) found in human subjects that both the action currents set up during muscle activity and the muscle sounds

indicated co-contraction as the rule in voluntary movement. Improvement in their techniques by other experimenters have confirmed these results. Tilney and Pike are particularly outspoken on behalf of co-contraction as the usual type of antagonistic activity. Using a tambour technique, they could only find simultaneous contraction during voluntary effort. From this they were led to define a muscle unit as a "physiological synergic group" consisting of "two anatomically opposed muscles, one which is dominant and the other the check element." They conclude that "simultaneous contraction is the rule in the great majority of cases in which muscles are voluntarily put in action." If these be the facts and if we are to retain "reciprocal innervation" as a basic principle in reference to voluntary muscle action, it would seem that its meaning should not be restricted to the simple type, involving concurrent relaxation of the antagonist.*

Several difficulties may be responsible for the seeming conflict in experimental findings: (a) the terminology of "simple" and "double" reciprocal innervation; (b) differences of techniques employed for the registration of muscle action; (c) the difficulty of controlling and analyzing voluntary movement.

> The analysis of voluntary movement is beset by so many difficulties, not the least of which is the uncertainty and the idiosyncrasies of the volitional process itself. (2, p. 453.)

Muscle action systems for experimental purposes can be regarded as presenting a hierarchy of functional complexity. At one extreme is pure reflex action where only one afferent nerve is stimulated; the result here seems to be simple reciprocal innervation. At the other extreme is the possibility of voluntarily contracting both antagonists at once or indeed whole systems of them. The latter may produce "fixation" of the mobile member or controlled oscillatory movements of varying rate and amount to meet the needs of motor adjustment. This range of complexity and the learning it involves probably constitutes the chief "idiosyncrasy" referred to above in regard to the volitional process. In any event some physiologists

> place more reliance upon the experiments performed on chronic spinal and decerebrate animals in which the tension relations of antagonistic muscles are

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* Experimenting with thalamic animals, Schoen (11) has reported, in the majority of cases, simultaneous contraction of the antagonistic muscles in such fundamental postural reflexes as the "Stützreaktion," produced by dorsiflexion of the digits. This is particularly interesting as it represents results from a preparation between the cortical and spinal levels.

directly measurable. Here, reciprocal innervation obtains undeniably, and the presence or absence of a cortex in all probability does not modify this fundamental plan of reflex organization. (2, p. 453.)

Whether or not physiological findings under rigid controls of spinal transection and decerebration are entirely free from ambiguity, the descriptions of muscular co-ordination contained in current psychological texts are not. On the whole these seem to incline towards acceptance, under all conditions, of inhibition of the antagonist during contraction of the protagonist, in other words simple reciprocal innervation. Three textual statements may be cited as examples:

a. It has been shown that whenever a motor impulse goes to a flexor causing its contraction, there goes also a neural impulse to the extensor muscle causing it to lengthen or relax. The muscles around a joint are thus set in opposed groups, one group relaxing while the other contracts. (Watson, J. B. "Psychology from Standpoint of a Behaviorist." (1924) p. 179.)
b. Flexion and extension of the same limb are interlinked (in the nerve centres) in such a way as to inhibit each other. (Woodworth, R. S. "Psychology." (Revised) p. 232.)
c. When one muscle of a pair of antagonists contracts, its opponent is less contracted than normally. This interesting, delicate and most important adjustment is termed *reciprocal innervation*. (Warren, H. C., and Carmichael, L. "Elements of Human Psychology." (Revised) p. 48.)

(ii) *Psychological Investigation*

Attempts have been made experimentally to investigate voluntary movement with special emphasis on the control of psychological factors. Such studies have been made with human subjects, approaching the muscle action system from its various segments, neural, muscular and motor. The central processes, for example, have been investigated psychologically by means of the reaction time type of experiment (12). This analysis is in terms of time and accuracy of response, supplemented by introspective evidence. Again, the characteristics of reciprocatory movement in an overt member have been studied with regard to amplitude, frequency and load, as for example, in voluntary flexion and extension of the wrist (13). The relationship between the time per mm. of a voluntary wrist stroke (called the "progression velocity") and the total amplitude attained was investigated; the results indicated that there was a very definite relationship of an inverse nature under various conditions of position, phase and load. Moreover, it appeared that the progression velocity in some way determined or at least was closely correlated with the amplitude of the stroke. These findings prompted the experimenter to ask, "What must be the conditions of muscle innervation and of muscle action which produce these characteristics in reciprocal voluntary movements?" On this

question, Dodge and Bott (14) reported a preliminary account of studies on the muscular action involved in various moving members using four antagonistic muscle systems of the body. The methods and technical difficulties of recording the action of muscles were previously dealt with by Dodge (15). Co-contraction of the antagonists was found to be the rule in all four muscle systems examined. It was indicated that further investigation was desirable to get conclusive evidence regarding the characteristics of muscular reciprocation in voluntary movement.

II. Statement of Problem

This research is a continuation of the type of study just mentioned. It endeavors to deal with the initiatory phases of voluntary movement in order to discover whether the antagonist relaxes or contracts at the commencement of such movement, and also the time sequence in terms of order and latency between the acting muscles. Accordingly, emphasis is placed primarily on the registration of the action of each of the opposed muscles and secondarily on resultant limb movement. The only account taken of the time of the neural impulse is through the careful control of the voluntary process by the customary procedures used in reaction time experiments.

The muscle groups chosen were the flexors and extensors of the right index finger of one adult trained subject. While such a study might be applied to various articulations of the body it was found that the requirements of precise instrumentation necessitated the narrow selection of subjects and musculature indicated above. This finger action system offers several advantages for analytical study: the movement is a well balanced one that is used extensively in daily tasks, which reduces the factor of learning to a minimum; the peripheral location of this member facilitates accurate analysis of the overt movement; the gross forearm musculature is relatively accessible for recording purposes and also for direct electrical stimulation, although the compact sheath of these muscles in the intact organism makes difficult the identification of their discrete action by mechanical or electrical means.

A. *Methods of Study*

Movements were controlled voluntarily under two major sets of conditions: Class I in which the subject adjusted in a prescribed manner to a changing external stimulus throughout the entire trial; Class II in which he voluntarily regulated the movement without reference to an outside control except the usual signal warning. Each of these classes of movement was of two types:

Class I. (a) Fixation against external resistance.
(b) Pursuit movements.

Class II. (a) Ballistic movements.
(b) Oscillatory movements.

I. (a) *Fixation Against External Resistance*

The subject, seated comfortably in an equipment, later described, which provided for full postural control and registration of movement, fixated his finger at an agreed zero point. This position was visually indicated to him by a pointer on a calibrated protractor. A graded load was then imposed against either flexors or extensors which would move the finger unless voluntarily resisted; the perception of this load prior to overt finger movement would be by kinesthetic clues only. Various loads of constant increment were used. In each trial the load commencing from a minimum, accepted as zero, was increased until the finger "broke"—a term used in this experiment to indicate that the finger was forced either up or down.

I. (b) *Pursuit Movements*

The subject under the same postural conditions as in (a) flexed or extended the finger in pursuit of a visible pointer under objective control.

II. (a) *Ballistic Movements*

The subject flexed or extended the finger in response to a spoken signal. The movement was initiated at maximum speed against constant known loads, the stroke being terminated by a mechanical cushioned stop.

II. (b) *Oscillatory Movements*

These movements differed from the ballistic type only in the fact that flexion and extension alternated at maximum speed through approximately thirty degrees, by the subject's own efforts without mechanical stops.

In addition to the above conditions, one series was recorded showing muscle and limb action resulting from peripheral faradic stimulation of graded intensity without voluntary interference.

These various types of voluntary movement were selected in order to ascertain whether the action of the antagonistic member of the synergic group shows uniformity, particularly in the initial stages, under these condition of central control, namely, zero movement, (fixation), slow controlled movement, fast explosive movement and fast reciprocating movement. These situations—except the electrical series, which presumes conscious relaxation—are accepted as instances of active voluntary control with a specific task to be performed, an initiation of movement or maintenance of

position by the subject himself with a high degree of conscious adjustment. In each case movement will be considered of each of three effector units of the action system, the protagonist muscle (prime mover), the antagonist muscle, and the moving limb.

B. *Controls*

The experimental controls may be conveniently described under the two headings:

(i) objective, consisting of the subject's postural control, attachments to muscles, the recording apparatus and the external devices for imposing known conditions upon the subject.

(ii) subjective, consisting of the general adjustment of the subject, control of attention, distraction, etc., and the specific instructions on tasks to be performed.

(i) *Objective Controls*

(1) Subject's Posture.—The subject was seated in a heavy metal adjustable chair of the Zander type. This chair was rigidly fastened to the recording apparatus to eliminate vibration. The subject's right forearm was pronated in a horizontal position with the elbow in a rest on the chair and the wrist fastened securely by an adjustable strap. The hand rested upon a wooden platform shaped to the fingers, leaving the index finger free to move. The hand was immobilized at 15 degrees of extension from the forearm axis, the fingers being flexed about 30 degrees (see figure 1). For recording movement, the index finger was encased in a padded metal cuff or splint. The cuff was mechanically attached to an axle in the line of the metacarpo-phalangeal joint (see figure 2), which operated the kymographic recording system: this axle also carried a pointer which visually indicated the angular movement of the finger on a concave protractor of ten-inch radius calibrated from the resting position in units of one degree. This moving system, constructed of aluminium, was counterbalanced and rendered as frictionless as possible. At one end of the axle a smooth metal plate was gripped by piano felt brakes whose pressure could be controlled in order to give a graded frictional load.

(2) Muscle Attachments.—Mechanically recording levers were used for registration, utilizing the thickening and thinning of muscle bulk as an indicator of shortening and lengthening during contraction and relaxation. The first point was how to connect with the muscles in order to convey this lateral displacement to

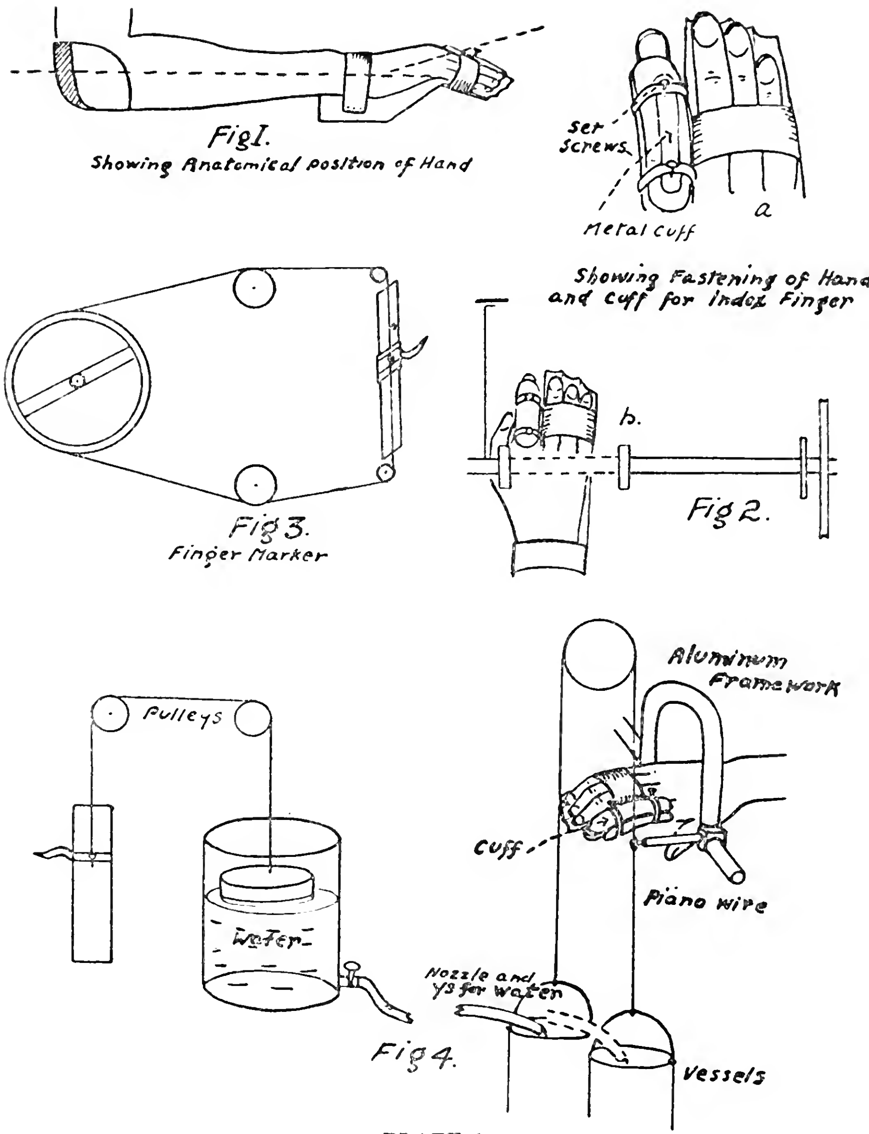

PLATE 1

Diagrams illustrating technique of controlling and registering finger movements.

the lever system. This was accomplishment by means of wooden thimbles one cm. square and shaped like a saddle in order not to slip off the muscles. These thimbles were imbedded deeply in the skin over the belly of the muscle at the point where previous palpation had revealed the maximum amount of thickening during contraction. They were kept in place by uniform pressure with elastic bands. As nearly as possible the same position on the muscle was used for successive trials in order that records might be comparable.

Criticism has been offered against mechanical registration as an indirect indicator of muscle activity based on structural and functional features of muscle groups. Thus it identifies muscle thickening with longitudinal displacement on the basis of the known constancy of volume of muscles. The presence of the lever or thimble on the muscle may conceivably interfere with its normal action. Experimental evidence on this question seems to indicate that levers of moderate pressure have no effect on the latency of muscle activity, although there may be a difference in the form of curve registered (15). The tissue environs constitute another unknown factor. An attempt to overcome this was made by lightly stretching the skin before applying thimbles and then imbedding them in a uniform way so that the effect of external tissue, if any, would at any rate be constant. The position of the thimble constituted another problem since relatively little is known about the progression of contraction along human muscle, particularly in synergic action, nor the order in which the various components of a muscle group come into action.* This was settled empirically, as suggested above, by placing the levers where the maximum displacement occurred and accepting this as representative of the muscle action of the group.

The criterion of satisfactory adjustment of subject and registration equipment was that the subject could not move his finger without moving the lever system attached to the muscles. Under passive movement of the subject's finger, however, the levers regularly showed no movement. Under slight voluntary effort it was possible to move the muscle lever without overtly displacing the finger; *i.e.*, the phenomena of voluntary action in muscles may occur below the level required for controlled limb movement, even with a member as light and mobile as the finger. This is in contrast with involuntary normal tremor which characterizes even the relaxed finger (17).

* See Travis, L. E., and Patterson, M. (16).

(3) Recording Apparatus.—This may be considered under two headings, (a) the leverage system which conveyed the muscle displacements from the thimbles to the markers; (b) the markers and kymograph.

(a) The leverage system: the thimbles having been imbedded vertically to the muscle fibres were clamped to light aluminium levers. These passed above and below the forearm at right angles to it and were pivoted on the framework in such a way as to maintain equal magnification of readings for both extensors and flexors. These aluminium levers were attached by adjustable swivel joints to longer levers of thin white pine at right angles to the thimble levers, *i.e.,* parallel with the forearm, which reached to the kymograph drum with suitable counter weights on the opposite end. This double leverage magnified the muscle thickening approximately fifty times and in the same direction as the actual thickening of the muscles. Thus the extensor lever on top of the arm and of the graph moved upward when the extensor muscle contracted and the flexor lever moved downward when the flexor contracted. When the muscles relaxed the levers followed from the constant tension with which the thimbles were held. By means of the threaded swivel joints it was possible to take up all loose play in the entire recording system and still allow it to work easily.

(b) The markers and kymograph: the markers were designed to overcome the familiar difficulty of interpreting tangential tracings, namely, by converting the angular swing of the horizontal wooden levers into vertical tracings. This was arranged as follows: A special unit, built of square brass bars, formed rigid guides for slides carrying the markers. These slides of smooth steel moved vertically and at right angles to the direction of the kymograph paper. A small hole was bored in the centre of each slide through which projected a stiff wire fastened to the end of the wooden lever. By this means the circular movement of the long levers was changed into a straight vertical tracing without appreciable distortion or friction. When the measurement of time relationships from tracings is a consideration this style of marker offers important advantages over the customary curved tracing.

The marker for finger movement similarly operated upon its own vertical slide but without levers. It has already been pointed out that the finger moved a mechanical system about the axis of the metacarpo-phalangeal joint. The rotation of this axle was conveyed to the finger marked by means of a stout silk thread which

was attached around a grooved wheel on the axle and passed as an endless belt over pulleys at the top and bottom of the marker slide (see figure 3). The marker for finger movement could be clipped to this thread at any desired height on the smoked record and would then oscillate up and down an exact distance (2 mm.) for each degree of arc that the finger extended or flexed. Thus all the markers for both muscles and the finger moved vertically and were set to clear each other by about half a millimeter when recording, which distance could be allowed for in measuring temporal relations. The frame which carried the markers could be tilted away from the record without disturbing the levers or silk belt, to permit changing kymograph papers.

The kymograph used in this study has previously been reported (13). It consisted of a rigid engine lathe base upon which was erected a horizontal kymograph driven by an adjustable speed motor; the limits of paper speed used in this investigation were 37.5 cm. per second for the fast records and 1 cm. per second for the slowest ones. The kymograph took a smoked paper about 3 meters long and 25 cm. wide. Time was recorded in the case of the fast records by a tuning-fork of 50 dv. per second and in the case of the slow ones by a seconds marker, which also provided a base line.

Each record thus represented graphically (a) time units; (b) movement of the index finger about the metacarpo-phalangeal joint, extension upward and flexion downward; (c) movement of the extensor muscle group, contraction being upward on the tracing; (d) movement of the flexor group, contraction downwards on the graph. All records were from right to left

(4) External Devices.—In addition to the controls described above, other mechanical features were used to provide special tasks for the subject. These tasks have been referred to as Fixation, Pursuit, Ballistic and Oscillatory Movements. The objective controls for these were as follows:

(a) Resistance, *i.e.*, fixation maintained against graded weights: From the framework which carried the finger splint a stiff rod was projected, equal in length to the index finger of the subject. The finger could then be passively moved by applying a force upward or downward to this rod (see figure 4). To the end of the rod was fastened a length of piano wire, reaching downward nearly to the floor and also upward over a pulley and thence again downward. On both ends of this wire were light metal containers of equal

weight, each with a capacity of about two and a half litres. These were in equilibrium, gravitationally, in their pull upon the rod. Loading either vessel would then exert a pull upon the finger proportional to the load and in order to maintain fixation of the finger either the extensors or flexors would have to operate voluntarily to sustain the added load. The load upon the finger was regulated by allowing water to flow silently at a constant rate into one or other of the containers; the rate of flow was set by the size of nozzle used, and a float in the cylindrical reservoir, level with the kymograph, recorded progressively by a vertical marker on the graph the volume of water that loaded the finger until the subject was compelled to "break" his fixation position. A sample record showing various rates of water flow and also the muscle action against a rapid load is shown in plate 2. Records obtained under the conditions show: time in seconds; the beginning and course of the increasing weight on the extensor or flexor muscles; the muscle action of the flexors and extensors whilst the load uniformly increases; and the finger movement of fixation until it "breaks" (see plate 2).

(b) Pursuit movements: The visual target which served as the pursuit object was a moveable pointer that traversed the calibrated protractor beside the finger pointer. The range of pursuit movement was twelve degrees on either side of the zero, *i.e.*, the resting position. The target pointer was oscillated at regular speeds by a variable speed motor and worm gear reducer which also operated a marker on the kymograph, thus objectively recording all excursions of the pointer. The range of speed was from .4 degrees per second to 7.1 degrees per second. As the target pointer moved, the subject endeavoured to move his finger synchronously with it, using as his clue the visible finger pointer which he tried to keep in superposition to the mechanically operated target pointer. Records obtained under conditions of pursuit showed, as in plate 3: time in seconds; the beginning and progress of motion of the pursuit pointer; the finger movement in pursuit; the extensor and flexor muscle action during such efforts.

(c) Ballistic movements: no extra mechanical controls were required for this except a firm rubber stop which terminated the flexion stroke of the finger. For the extension stroke, the articulation being not so great, no such stop was used but the finger was allowed to proceed to its maximum displacement. Three loads were provided by means of the friction brake described above. These

frictional loads were equated to gravitational loads in grams imposed at a distance of 10 cm. from the centre of movement of the finger. The loads were of three dimensions, 20 grams, 275 grams and 550 grams, and were selected in terms of the subject's report on kinaesthetic evidence as being zero, medium and maximum. Records obtained under these conditions as in plate 4, showed: a tuning fork time line, 50 dv. per second, the finger movement, the extensor and flexor muscle action during the trial.

(d) Oscillatory movements: these movements were similar to the previous type, the extent of movement being about 30 degrees of amplitude regulated voluntarily by the subject without mechanical stops, but using kinaesthetic control supplemented by visual perception of terminal points for the prescribed movement shown on the protractor over which the finger pointer moved.

(e) Non-voluntary movements: these were initiated by faradic stimulation of the extensor indicis proprius as its motor point, (a similar flexor stimulation was not found to be obtainable without involving more than the index finger). To the subject's left upper arm was attached an indifferent electrode, consisting of a saline pad about 100 sq. cm. in area, kept uniformly saturated, and enclosed in a zinc holder. The stimulus electrode was a brass rod covered with a saline saturated chamois. This was held firmly by clamps against the motor point on the right forearm which was empirically determined. Current was provided from the secondary coil of a variable inductorium, the primary coil of which was energized by a $1\frac{1}{2}$ volt dry cell. Stimuli of weak, medium and strong intensity were administered, the first barely moving the finger, the medium briskly moving it and the strong convulsively moving it with manifest radiation into other muscle groups. Records obtained under these conditions showed: tuning-fork time; the finger movement; the beginning and duration of electrical stimulation; the muscle action of extensors and flexors.

(ii) *Subjective Controls*

The subject was posturally adjusted to suit the mechanical requirements of the registration system as regards position of elbow, wrist, hand and fingers, the tension of straps being arranged by the subject, who also cooperated in arranging the tension of thimbles on the muscles. Before each trial, special care was taken to check that the muscle markers responded freely for the slightest voluntary movement of the finger; until this test was met the mechanical

adjustments would not be accepted as satisfactory. The subject practised relaxing as completely as possible when the finger rested at the zero position on the protractor scale. Practice trials were always given before a record was taken. Instructions to the subject were as follows:

(a) Fixation: "After the signal 'Ready' you will presently feel a load pulling on your index finger; please resist this just sufficiently to keep your finger at the zero position as long as you can." No indication was given as to whether the traction would be against the flexors or the extensors; the subject was left to determine this kinesthetically. It was reported sometimes to be first detected by visual perception of a slight movement of the finger pointer off the zero point of the scale, but in at least some such cases the muscles had previously begun to react appropriately.

(b) Pursuit: "Observe this target pointer. When you see it move I want you to follow it with your finger keeping the finger pointer exactly over it. Follow it as carefully as you can even if it reverses its direction."

(c) Ballistic: "After the warning 'Ready,' when I say 'Go,' move your finger downward (or upward, as the case required) as rapidly as you can and as far as you can go."

(d) Oscillatory: "When I say 'Ready—Go,' begin to oscillate your finger as fast as possible about 30 degrees (demonstrated visually by the finger pointer) and continue until told to stop. Begin with extension (or flexion, as the case required)."

(e) Non-voluntary: "Relax as completely as possible at the zero position; a light electrical stimulus will be applied to your arm. In this experiment you are asked to do nothing but to remain relaxed." In this series electrical stimulations were first given below the response threshold and then with greater intensity in order to permit the subject to remain as relaxed as possible through a number of trials. Only a few readings were taken each day as tension on the part of the subject often remained after strong stimulation. Ample time was allowed between trials for the subject to relax the muscles as nearly as might be to their original position as shown by the markers.

In all the above experiments an attempt was made to prevent or reduce distraction of the subject from his task by screening from his view the recording mechanism and other external controls. Auditory clues were rendered non-indicatory by operating the driving controls continuously.

III. Treatment of Results

The kymograph records obtained under the above conditions were analyzed from three points of view, direction of initial action of muscles, time relations, and the "angle" of muscle records. Special importance for our purpose attaches to the *direction* of the antagonistic muscle action during voluntary movement or fixation because, as previously pointed out, if the gross action of the antagonist is one of relaxation during active contraction of the prime mover, then the type of integration is that of "simple" reciprocal innervation. If, on the other hand, the gross action of the antagonist is contractive, the integration is not of the "simple" type, though it may represent "double" reciprocal innervation in the summation sense. Time intervals and sequences between the stimulus, prime mover, antagonist and finger are noted also for evidence regarding whether or not the type of reciprocation is "simple," since in all the reports on simple reciprocal innervation mentioned above, relaxation of the antagonist is practically simultaneous with contraction of the protagonist. A third type of analysis concerns the "angle" formed on the record by the antagonistic muscle. If this is steep, the muscle came into action suddenly, if gradual, muscle action was slower. This analysis is useful in objectively differentiating voluntarily initiated reactions from non-voluntary ones. No account was taken of the absolute height of the muscle response records because the relationship between actual pull on its tendon of insertion and amount of muscle thickening as communicated to an impressed thimble is not known or discoverable by the mechanical method here employed.*

A total of 260 records were studied which fall under the following classes:

(a) *Resistance against load:*

16 records of flexor load;
11 " " extensor load.

* This relationship may vary with different intensities or speeds of action and it is also complicated by the fact that a wave of contraction moves along the muscle in a proximal-distal direction or under some conditions from a mid location in both directions (16). This aspect of the problem requires further study with combined methods such as those of action currents and mechanical levers. Three thimbles working simultaneously at longitudinally discrete points on the forearm musculature will each respond to extension of the index finger but in sequence rather than simultaneously. This likewise suggests progression of a wave of voluntary contraction along the muscle.

(b) *Pursuit Records:*

26 records of flexion pursuit;
24 " " extension pursuit.

(c) *Ballistic Records:*

28 records of flexion, (zero load);
27 " " extension, (zero load);
12 " " flexion, (medium load, 275 gms.);
18 " " extension, (medium load, 275 gms.);
18 " " flexion, (maximum load, 550 gms.);
16 " " extension, (maximum load, 550 gms.).

(d) *Oscillatory Records:*

5 records flexion (zero load);
6 " extension (zero load).

(e) *Electrical Records:*

35 records extensor stimulations, (zero load);
13 " " " (medium load);
5 " " " (maximum load).

The tracings were measured over a lamp box with glass top. Initiation of movement (for finger or muscles) was taken to be the point where the recorded line first appreciably diverged from the horizontal as indicated by a straight edge parallel to the base line. Since muscle thickening was magnified 50 times and since 1 degree of finger movement displaced the record 2 mm., this criterion was accepted as sufficiently accurate for each, as showing the commencement of muscle or finger action respectively. Raw measurements thus obtained were corrected for lateral displacements of the markers as determined by test markings taken on the stationary record prior to each day's trials. All time records quoted in the tables are corrected measurements. The results will be dealt with under the classification of movements outlined above.

IV. Analysis of Results

A. *Fixation Against Resistance—Flexor Load*

Table Ia shows the results from the subject's fixation against an increasing flexor load beginning from zero. Column 1 gives the serial record order as stated in grams per second in column 2. Columns 3 and 4 give respectively for the protagonist (F = flexor) and the antagonist (E = extensor), the direction of activity, the reaction time from beginning of load and the order of action. Column 5 states the latency between the action of the two muscles; columns 6 and 7 give respectively the absolute load in grams at the beginning of action of the first and second muscle. Column 8 notes whether the finger moved ("break") and column 9 gives the absolute load at the instant of "break" or the end of the record, the maximum load being about 2430 grams.

Table Ib gives similar results for extensor loads, the protagonist being now the extensor (E) and the antagonist the flexor (F).

Analysis of Fixation Results

(a) Direction of muscle action: it will be seen that in cases of voluntary resistance to increasing load *both muscle systems are invariably active and this activity is always contractive.* At no stage of the contraction of the protagonist does the antagonist show relaxation.

(b) Time relationships: (i) The time intervals between the initial action of the opposed muscle shown in columns 5 for both flexor and extensor loads, are in most cases much too great to indicate simple reciprocal innervation which approximates simultaneity. Attention is directed to the first record in table Ib where the time elapsing between the action of the protagonist and the antagonist is more than 25 seconds. Such a dissociation in the action of the two muscles, aside from the contractile direction of their action, is scarcely compatible with Sherrington's statement (page 3), that the responses of the two antagonists "are part and parcel of the same reflex action." One might conceivably assume on the principle of summation that this inaction was a resultant of positive and negative tendencies which operated in balance for this considerable period, but this would not represent simple reciprocal innervation.

(ii) The latency time between the two muscle systems, shown in column 5, show a rough progression. This can be emphasized by

TABLE Ia

Fixation Movement—Flexor Load

(1)	(2)	(3)			(4)			(5)	(6)	(7)	(8)	(9)
		PROTAGONIST = F			ANTAGONIST = E							
Number	*Rate of Load in grams per second*	*Direction of Action C = contr. R = relax.*	*Time of Action in seconds after load*	*Order of muscle's action i = 1st. ii = 2nd. * = simult.*	*Direction of Action C = contr. R = relax.*	*Time of Action in seconds after load*	*Order of muscle's action i = 1st. ii = 2nd. * = simult.*	*Time between first and second muscles*	*Load in grams at first muscle action*	*Load in grams at second muscle action*	*Remarks*	*Limit of load or end of record (in grams)*
1	43	C	2.87	i	C	10.30	ii	7.43	129	443	No finger break	2430
2	74	C	1.86	*	C	1.86	*	0	135	135	" " "	2430
3	82	C	2.25	i	C	2.48	ii	.23	185	204	Slight break at	1665
4	82	C	2.26	i	C	9.96	ii	7.00	204	815	Fi. before F by 2.15″ then no break until	2430 (break)
5	85	C	4.50	i	C	6.32	ii	1.82	370	537	Finger break at	1610
6	87	C	2.22	i	C	8.79	ii	6.57	189	760	" " "	2349
7	102	C	1.42	i	C	8.72	ii	7.3	148	890	No finger break	2430
8	111	C	3.20	i	C	3.38	ii	.18	360	378	Fi. before F by .27″ then no break	2430
9	111	C	3.70	i	C	3.88	ii	.18	407	425	No finger break	2430
10	114	C	.35	*	C	.35	*	0	37	37	Finger break	1295
11	114	C	.73	ii	C	.96	i	.23	82	111	" "	1258
12	115	C	2.1	i	C	6.86	ii	4.76	232	790	No finger break	2430
13	122	C	1.68	*	C	1.68	*	0	204	204	" " "	2430
14	122	C	1.18	*	C	1.18	*	0	125	125	" " "	2430
15	126	C	.09	ii	C	.36	i	.28	11	46	" " "	2430
16	129	C	1.62	i	C	6.06	ii	4.44	205	785	" " "	2430

Showing rate of increment of flexor load; direction and time of both muscle actions; absolute loads and type of finger action. Protagonist = Flexor (F); Antagonist = Extensor (E); Fi. = Finger.

TABLE IIb

Fixation Movement—Extensor Load

(1)	(2)	(3)			(4)			(5)	(6)	(7)	(8)	(9)
		PROTAGONIST = E			ANTAGONIST = F							
Number	*Rate of Load in grams per second*	*Direction of Action C = contr. R = relax.*	*Time of Action in seconds after load*	*Order of events; x = with load i = 1st. ii = 2nd. * = simult.*	*Direction of Action C = contr. R = relax.*	*Time of Action in seconds after load*	*Order of events; x = with load i = 1st. ii = 2nd. * = simult.*	*Time between first and second muscles*	*Load in grams at first muscle action*	*Load in grams at second muscle action*	*Remarks*	*Limit of load or end of record (in grams)*
1	18	C	1.82	i	C	27.53	ii	25.71	37	508	No finger break	950
2	30	C	1.70	*	C	1.70	*	0	35	35	Finger break	795
3	52	C	0	x	C	10.86	ii	10.86	0	555	" "	980
4	52	C	1.86	i	C	10.96	ii	9.1	97	570	" "	925
5	80	C	1.30	i	C	5.50	ii	4.2	104	436	Fi. before E by .28″	647 (break)
6	85	C	0	x	C	8.5	ii	8.5	0	703	Finger break	907 (break)
7	93	C	2.18	i	C	2.27	ii	.09	222	241	Fi. before E by 2.09″	500 (break)
8	93	C	3.55	i	C	8.50	ii	4.95	330	793	" " " " 3.2″	1165 (break)
9	114	C	1.05	i	C	6.65	ii	5.6	118	760	" " " " .25″	961 (break)
10	122	C	.7	i	C	5.99	ii	5.29	80	734	" " " " .18″	907 (break)
11	122	C	.58	i	C	5.98	ii	5.4	71	735	No break	1200 (break)

Showing rate of increment of extensor load; direction and time of both muscle actions; absolute loads and type of finger action. Protagonist = Extensor (E); Antagonist = Flexor (F); Fi. = Finger.

taking the average of these time intervals for the slower half of the records and comparing it with the average for the faster half; such a comparison is as follows:

Flexor Load		*Extensor Load*	
Av. Latency in seconds Records No. 1 to No. 8	*Av. Latency in seconds Records No. 9 to No. 16*	*Av. Latency in seconds Records No. 1 to No. 5*	*Av. Latency in seconds Records No. 7 to No. 11*
3.82 ± 3.26	1.24 ± 1.68	9.97 ± 4.65	4.27 ± 1.45

This lends support to the principle that *the slower the rate of increment of load the greater the temporal dissociation of the antagonistic muscle systems. Such a principle extends to the* more general one that characteristics of muscle reciprocation are due in part to the nature of the external task.

(iii) Certain irregularities of time relationships are also evident in the data. Thus it is noted that the order of the acting units is variable; moveover, if records showing similar order of muscle action are examined it is found that the time intervals between the units are again variable. These irregularities, however, exhibit certain general trends. Thus, for example, there is a predominating order of events for both flexor and extensor loads, although this order differs respectively. This can be seen as follows in terms of 16 and 11 cases:

Order of Acting Units	*Percentages of cases*	
	Flexor Load (16 cases)	*Extensor Load (11 cases)*
1. Load; 2. Protagonist; 3. Antagonist	55%	73%
1. Load; 2. Antagonist; 3. Protagonist	25%	0%
1. Load; 2. Protagonist & Antagonist simult.	20%	9%
1. Load & Protagonist simult.; 2. Antagonist	0%	18%

It is seen that in flexor fixation the antagonist usually succeeds the protagonist but precedes or equals it nearly as often, whereas in extensor fixation the antagonist never precedes and rarely coincides with the protagonist.

In fixation loads the tendency on the whole is for the time interval between the inception of load and the beginning of the first

muscle action to be shorter and more regular than the latency between the action of the two muscles. Here again there are differences in the findings for flexor and extensor loads:

	Flexor Load	*Extensor Load*
Time in seconds between load and first muscle (column 4, Tables IA and IB)	2.00 ± .95	1.34 ± . 89
Time in seconds between first and second muscles (column 5)	2.53 ± 2.50	7.24 ± 4.46

The factors underlying these variations are not evident from the data. It may be conjectured that the degree of "readiness" on the part of the subject with the accompanying tonicity of the muscles at the inception of the load contributes to the irregularities.

(c) A striking qualitative feature of the fixation records is the step-wise manner in which both muscles, but more particularly the protagonist, increase their contraction in response to a smoothly graded load (Plate 2). These steps are less frequent and smaller the slower the load and further exploration might reveal some connection between them and the rate of load increment. Except in the case of large steps they do not synchronize in the opposed muscles. And the tracings also show regions of contraction that are not step-wise in both muscles, especially at the upper limits of fast loads as in Plate 2b. Such a step-wise progression may indicate that under these conditions antagonistic muscles increase their force for the most part by succeeding "volleys" of energy rather than by a gradually increasing contraction. This phenomenon also shows that the term "relaxation" is relative, since each of the indicated steps presents a situation analogous to that at the originally accepted relaxation point, namely, the beginning of the load.

To summarize: The type of muscular co-ordination involved in supporting a smoothly increasing load is not that of simple but of double reciprocal innervation. Two types of evidence support this conclusion, first, the direction of the antagonistic muscle response, which is always contractive; secondly, the long latencies between the initial activity of the two muscle systems. The reported irregularities in the time relations and the step-wise quality of the muscle responses offer problems for further investigation.

B. *Pursuit Movements*

Table IIa shows the results of voluntary pursuit of a visual pointer in the direction of flexion at various rates of speed as shown graphically in plate 3.

TABLE IIa
Pursuit in direction of flexion

(1) No.	(2) *Pursuit pointer speed per sec.*	(3) *No. 1 Unit*		(4) *Time in sec.*	(5) *No. 2 Unit*		(6) *Time in sec.*	(7) *No. 3 Unit*		(8) *Time in sec.*	(9) *No. 4 Unit*	(10) *Remarks*
1	.41°	E	C	2.24	F	C	.06	P		1.56	Fi.	Anticipatory muscle action
2	.63	E	C	.19	P		.77	F	C	.68	"	
3	.84	E	C	.18	P		.41	F	C	.32	"	
4	1.26	P		.36	E	C	.06	F	C	.09	"	
5	1.26	P		.14	E	C	.06	F	C	.19	"	
6	1.47	P		.32	E	C	.19	F	C	.13	"	
7	1.47	E	C	.27	P		.06	F	C	.16	"	
8	1.47	P = E	C				.25	F	C	.06	"	
9	1.47	P		.06	E	C	.27	F	C	.24	"	
10	1.68	P = E	C				.43	F	C	.27	"	
11	2.31	E	C	.15	F	C	.72	P		.15	"	"
12	2.31	P		.35	E	C	.09	F	C	.31	"	
13	2.31	E	C	.43	P		.06	F	C	.18	"	
14	2.31	P		.08	E	C	.09	F	C	.39	"	
15	2.31	P		.75	E	C	.16	F	C	.53	"	
16	2.42	E	C	1.00	P		.40	F	C	.08	"	
17	2.52	P		.12	E	C	.12	F	C	.17	"	
18	2.94	P		.07	E	C	.15	F	C	.12	"	
19	3.36	P		.09	E = F	C	.00			.06	"	
20	3.78	P		.07	E	C	.08	F	C	.14	"	
21	4.91	E	C	.75	P		.25	F	C	.32	"	
22	5.67	E	C	.25	P		.25	F	C	.10	"	
23	6.72	P		.25	E = F	C	.00			.36	"	
24	6.93	P		.24	E = F	C	.00			.12	"	
25	6.93	P		.30	E = F	C	.00			.12	"	
26	7.14	P		.12	E	C	.07	F = Fi.	C			

Records are ranked in order of speed of pointer. All records show action of a contractile nature in both muscle systems. Time is quoted in seconds.

P = pointer that subject is attempting to pursue.
E = action of extensor group of muscles.
F = " " flexor " " "
Fi = finger movement.
C = contraction.
R = relaxation.

See text for detailed explanation.

TABLE IIb
Pursuit in direction of extension

(1) *No.*	(2) *Pursuit pointer speed per sec.*	(3) *No. 1 Unit*		(4) *Time in sec.*	(5) *No. 2 Unit*		(6) *Time in sec.*	(7) *No. 3 Unit*		(8) *Remarks*
1	.84°	E	C	.59	Fi		...	..		No flexor movement
2	1.26	"	C	.62	"		1.25	F	C	Delayed flexor "
3	1.26	"	C	.64	"		.21	F	C	
4	1.47	"	C	.45	F	C	.16	Fi		
5	1.47	"	C	.21	Fi		.13	F	C	
6	1.47	"	C	.14	"		.14	F	C	
7	1.47	"	C	.45	"		...	...		No flexor movement
8	1.68	"	C	.75	F = Fi	C				
9	2.31	"	C	.06	Fi					" " "
10	2.31	"	C	.15	"					" " "
11	2.31	"	C	.12	"					" " "
12	2.31	"	C	.10	"		.06	F	C	Very slight flexor movement
13	2.31	"	C	.22	F	C	.44	Fi		
14	2.42	"	C	.07	"	C	.47	Fi		
15	2.52	"	C	.05	Fi		.17	F	C	
16	2.94	"	C	.03	F	C	.31	Fi		
17	3.36	"	C	.23	Fi		.06	F	C	
18	3.78	"	C	.04	F = Fi	C				
19	4.41	"	C	.06	Fi		.03	F	C	
20	5.67	"	C	.15	F = Fi	C				
21	6.72	"	C	.03	Fi		.05	F	C	
22	6.93	"	C	.07	F = Fi	C				
23	6.93	"	C	.09	Fi		.09	F	C	
24	7.14	"	C	.09	"		.13	F	C	

Records are ranked in order of speed of position.
19 out of 24 records show antagonistic contraction;
5 " " " " " no " " ;
No records show a relaxation of antagonists. Time is quoted in seconds. Pointer records were rejected in this series as unreliable.

F = flexor action.
E = extensor action.
Fi = finger movement.
C = contraction.
R = relaxation.

See text for detailed explanation.

Column 1 gives a serial numbering of the records arranged in order of increasing speed; column 2 states the speed of the target pointer in degrees of movement per second; columns 3, 5, 7, 9 show the order in which the four units respectively came into action, *i.e.*, the pointer, the flexor muscles, the extensor muscles and the finger; these columns also indicate whether the muscle action was of contraction or relaxation. Columns 4, 6, 8 give the time intervals between the four units in their order of occurrence.

Table IIb shows the results from voluntary pursuit of a target pointer in direction of extension, this being a reversal from flexion pursuit rather than a movement initiated from a position of full relaxation.

In these trials it was found not possible accurately to determine the beginning of the target pointer's movement. Accordingly, only three units, extensor, flexor and finger, are reported. Otherwise tables IIa and IIb are comparable.

Analysis of Results of Pursuit Movement

(a) Direction of muscle action: Table IIa shows that both muscle systems invariably acted during voluntary pursuit in the flexion direction. Table IIb shows that both muscle systems acted in 79% of the cases during voluntary pursuit in the extension direction. *In these instances activity was always contractile in direction* in the initial stages of finger movement.

A probable explanation of the failure of the antagonist to act in certain cases of extension pursuit is that the mechanical controls were not fully comparable with those of flexion. All the pursuit records began in the direction of flexion and the target pointer after reaching its downward limit remained stationary for one to two seconds and was then moved upward for extension. This pause did not allow sufficient time for the muscles to relax to their initial level. Accordingly, the muscles are partially and unequally contracted at the initiation of extension pursuit. Under these conditions one-fifth of our cases of extension pursuit show slight amounts of flexor relaxation during the period of extensor contraction. This relaxation does not occur at the initiation of finger movement but occasionally during such movement. The principle previously enunciated we feel is not affected by these instances, namely, that when the antagonist first moves it does so in the direction of contraction.

(b) Time relationships: The latency between the action of the two muscle systems again represent longer periods than for simple

reciprocal innervation being as long as 2.24 seconds in one instance. In the case of flexion pursuit the average interval between the two muscle systems is .37 sec. ± .37 and in the extension pursuit is .33 ± .27. These latencies as shown in tables IIa and IIb indicate a tendency towards a progression depending on the speed of target pointer, this being more evident in the case of extension. Thus the correlations (r) between speed of pointer and antagonistic latency are – .92 ± .029 and – .59 ± .127 in the case of the extension and flexion records respectively. These correlations are interpreted to mean that the more slowly antagonistic muscles are called upon to act the greater is the dissociation in time of their initial action.

There is again irregularity in the time and order of muscle action. The gross mean deviations from the averages shown above (.37 ± .37; .33 ± .27;) denote the variability in time. The order of occurrence classified according to types is as follows:

Order of units	*Percent of cases*	
	Flexion 26 cases	*Extension 24 cases*
1. Antagonist 2. Protagonist 3. Finger	85	0
1. Muscles simultaneously 2. Finger	15	0
1. Protagonist 2. Finger 3. Antagonist	0	58
1. Protagonist 2. Antagonist 3. Finger	0	21
1. Protagonist 2. Finger and Antag. simult.	0	21

It will here be noted that in pursuit the extensor muscle moves first or simultaneously with the flexor in all cases, for both flexion and extension. As was found in fixation (*supra*, p. 27), there are no cases of extension where the antagonist moved first. On the contrary, for flexion 85% of the cases show that the antagonist moved first, and fixation records showed 25% of such antagonistic priority. This may indicate merely that the extensor muscle system is more unstable than the flexor system and tends always to act first whatever the direction of the overt movement. Or it may have adaptive significance for coordinated action, namely, that the extensor system, being the weaker, is allowed an appropriate handicap over its antagonist.

(c) Qualitative analysis of records: (i) The "angle" shows a characteristically sharp break for both of the antagonists, which is nearly as abrupt for medium as for fast speeds (plate 3). This seems to be typical of voluntary muscle action. (ii) Similar stepwise increases in tension occurred in muscle action during pursuit

as was shown in the fixation series. Under our conditions this character was most marked in the flexion records. This further suggests the "volley" type of contraction as was previously mentioned.

Table IIa shows in 8% of the cases both muscle systems acted prior to movement of the visual target pointer, and in 27% *one* of the muscle systems acted in advance of the pointer. Since the subject was aware in advance of the direction the target pointer was to move, these instances seem to offer objective evidence of the muscular phase of "readiness," said to be characteristic of the "fore-period" that precedes any voluntary reaction (18). It may be noted too that the extensor muscle predominantly assumes this favorable "set" even when the movement is to be one of flexion.

The results from voluntary pursuit of an externally moved target substantially agree with those for fixation, *i.e.*, the type of muscular co-ordination in the initiation of movement is not that of simple reciprocal innervation. The direction of contraction and period of latency between the muscles both support this conclusion, although the temporal dissociation is not nearly as great as in the fixation records. There is evidence, however, that under conditions of marked contracture movement may be sustained with relaxation of the antagonist during contraction of the protagonist.

Our evidence concerning muscular set or readiness during the fore-period of reaction would require further elaboration before significant conclusions could be drawn.

C. *Ballistic Movements*

Table IIIa gives the results of 28 flexion finger movements from rest through 30 degrees to a stop, with zero load, and at maximum speed. Column 1 gives the serial numbering in order of average velocity in degrees per second as in column 2; columns 3, 5 and 7 name the order of initial action of the three units, respectively, and columns 4 and 6 give the time intervals between these units in sigmata.

Table IIIb gives the results of 12 cases of flexion against a medium load, and Table IIIc gives the results of 18 cases of flexion under maximum load.

Three additional sets of results were obtained for extension movements under the same loads. These are shown in tables IVa, IVb, IVc.

TABLE IIIa

Ballistic Movement—Flexion—Zero Load

(1) No.	(2) Finger Speed Degrees per Sigma	(3) No. 1 Unit	(4) Time in Sigmata	(5) No. 2 Unit	(6) Time in Sigmata	(7) No. 3 Unit
1	.229	F	4	E	5	Fi.
2	.225	"	35	Fi.	24	E
3	.213	"	5	"	37	"
4	.200	"	7	"	10	"
5	.197	"	17	"	5	"
6	.187	F = E			17	Fi.
7	.185	F	16	E	8	"
8	.180	"	25	Fi.	3	E
9	.176	"	6	"	29	"
10	.174	F = E			8	Fi.
11	.170	F = Fi.			29	E
12	.170	*E	13	F = Fi.		
13	.170	F	17	F	3	E
14	.169	"	9	"	16	"
15	.166	"	17	"	5	"
16	.166	"	13	E	21	Fi.
17	.164	"	8	E = Fi.		
18	.163	F = Fi.			3	E
19	.161	F	9	Fi.	21	"
20	.160	"	21	E	16	Fi.
21	.159	"	33	Fi.	11	E
22	.159	"	14	"	27	"
23	.158	"	11	"	16	"
24	.157	"	17	E	18	Fi.
25	.156	"	9	E = Fi.		
26	.156	"	28	E = Fi.		
27	.152	"	7	E	5	"
28	.145	"	9	E	11	"

Showing order of action units and time interval in sigmata during initiation of ballistic movements, flexion in direction and against zero load. All muscle actions were of contraction; none was of relaxation.

F = Flexor; E = Extensor; Fi = finger.

* Antagonist moved first.

TABLE IIIb
Ballistic movement—Flexion—Medium load

(1) No.	(2) Finger Speed Degrees per Sigma	(3) No. 1 Unit	(4) Time in Sigmata	(5) No. 2 Unit	(6) Time in Sigmata	(7) No. 3 Unit
1	.100	F	13	E	29	Fi.
2	.096	F = E			42	"
3	.096	F	8	"	54	"
4	.091	"	20	"	30	"
5	.089	"	49	"	31	"
6	.084	"	23	"	46	"
7	.083	"	13	"	41	"
8	.071	"	10	"	52	"
9	.066	"	27	"	40	"
10	.065	"	52	"	42	"
11	.064	"	23	"	45	"
12	.064	"	31	"	38	"

Showing order of action units and time intervals, in sigmata, during initiation of ballistic movements, flexion in direction against medium load, 275 grams. All muscle actions were of contraction; none was of relaxation.
F = Flexor; E = Extensor; Fi = Finger.

TABLE IIIc
Ballistic movements—Flexion—Maximum load

(1) No.	(2) Finger Speed Degrees per Sigma	(3) No. 1 Unit	(4) Time in Sigmata	(5) No. 2 Unit	(6) Time in Sigmata	(7) No 3 Unit
1	.101	F	24	E	35	Fi.
2	.091	"	3	"	47	"
3	.087	"	28	"	40	"
4	.087	"	5	"	50	"
5	.083	"	16	"	63	"
6	.081	"	7	"	63	"
7	.080	F = E			68	"
8	.074	F	11	"	32	"
9	.073	"	21	"	50	"
10	.072	"	7	"	69	"
11	.064	"	100	"	40	"
12	.059	"	16	"	57	"
13	.051	"	69	"	124	"
14	.048	"	61	"	100	"
15	.047	"	8	"	55	"
16	.044	"	15	"	90	"
17	.035	E	4	F	37	"
18	.035	"	6	"	48	"

Showing order of action units and time intervals, in sigmata, during initiation of ballistic movements, flexion in direction against maximum load, 550 grams. All muscle actions were of contraction; none was of relaxation.
F = Flexor; E = Extensor; Fi. = Finger.

TABLE IVa
Ballistic Movements—Extension—Zero Load

(1) No.	(2) Finger Speed Degrees per Sigma	(3) No. 1 Unit	(4) Time in Sigmata	(5) No. 2 Unit	(6) Time in Sigmata	(7) No. 3 Unit
1	.223	E	14	Fi.	40	F
2	.221	"	26	"	32	"
3	.178	"	23	"	21	"
4	.174	"	19	"	27	"
5	.174	"	28	"	5	"
6	.172	"	20	"	24	"
7	.170	"	19	"	19	"
8	.170	"	36	"	55	"
9	.169	"	36	"	21	"
10	.169	"	23	"	24	"
11	.168	"	32	"	9	"
12	.167	"	15	"	37	"
13	.167	"	29	"	24	"
14	.165	"	21	"	21	"
15	.165	"	29	Fi. = F		"
16	.165	"	29	Fi.	16	"
17	.163	"	21	"	27	"
18	.162	"	39	"	13	"
19	.158	"	32	"	23	"
20	.157	"	29	"	33	"
21	.155	"	32	"	27	"
22	.155	"	29	"	19	"
23	.154	"	29	"	29	"
24	.153	"	24	"	39	"
25	.140	"	10	"	17	"
26	.129	"	5	"	13	"
27	.123	"	9	"	29	"

Showing order of action units and time interval in sigmata during initiation of ballistic movements, extension in direction and against zero load. All muscle actions were of contraction; none was of relaxation.

F = Flexor; E = Extensor; Fi. = Finger.

TABLE IVb
Ballistic Movements—Extension—Medium Load

(1) No.	(2) Finger Speed Degrees per Sigma	(3) Unit No. 1	(4) Time in Sigmata	(5) No. 2 Unit	(6) Time in Sigmata	(7) No. 3 Unit
1	.093	E	35	F	29	Fi.
2	.091	"	32	"	11	"
3	.088	"	42	"	13	"
4	.086	"	58	"	5	"
5	.079	"	92	Fi.	25	F
6	.078	"	69	"	8	"
7	.077	"	56	F	29	Fi.
8	.076	"	50	"	19	"
9	.071	"	60	"	8	"
10	.070	"	32	"	24	"
11	.067	"	27	"	35	"
12	.064	"	72	Fi.	16	F
13	.062	"	69	"	9	"
14	.062	"	70	"	30	"
15	.061	"	81	"	11	"
16	.052	"	42	F	24	Fi.
17	(no speed recorded)	"	71	"	5	"

Showing order of action units and time intervals, in sigmata, during initiation of ballistic movements, extension in direction against medium load, 275 grams. All muscle actions were of contraction; none was of relaxation.
F = Flexor; E = Extensor; Fi. = Finger.

TABLE IVc
Ballistic Movement—Extension—Maximum Load

(1) No.	(2) Finger Speed Degrees per Sigmata	(3) No. 1 Unit	(4) Time in Sigmata	(5) No. 2 Unit	(6) Time in Sigmata	(7) No. 3 Unit
1	.075	E	47	F	29	Fi.
2	.071	"	67	"	43	"
3	.070	"	44	"	19	"
4	.069	"	67	"	14	"
5	.067	"	43	"	19	"
6	.065	"	34	"	31	"
7	.065	"	60	"	40	"
8	.064	"	64	"	5	"
9	.063	"	56	"	11	"
10	.059	"	54	"	7	"
11	.059	"	30	"	22	"
12	.058	"	34	"	19	"
13	.055	"	56	"	38	"
14	.055	"	58	"	54	"
15	.046	"	57	"	39	"
16	.041	"	52	"	29	"

Showing order of action units and time intervals, in sigmata, during initiation of ballistic movements, extension in direction against maximum load, 550 grams. All muscle actions were of contraction; none was of relaxation.
F = Flexor; E = Extensor; Fi. = Finger.

Analysis of Results—Ballistic Movements

(a) Direction of muscle activity: Both muscle systems invariably act during voluntary ballistic movement and this activity is always in the direction of contraction on the part of the both muscles.

(b) Temporal relationships: (1) The time intervals between the antagonist and protagonist show smaller periods of latency in the ballistic type of movement than in either of the former types. They are, however, sufficiently great to differ from the brief latency of a simple reciprocal activity. The data are:

Load	*Average time intervals in sigmata*	
	Flexion	*Extension*
Zero	21 ± 11	48 ± 10
Medium	22 ± 13	62 ± 22
Maximum	11 ± 18	51 ± 9

The latency for the flexion records is consistently smaller than that for extension. There does not seem to be any consistency or progression in terms of the three loads used.

(ii) The order of the acting units is as follows:

Order of Units	*Percent of Cases*					
	Flexion			*Extension*		
	Zero	Med.	Max.	Zero.	Med.	Max.
1. Protagonist; 2. Antag.; 3. Finger	54	0	0	96	35	0
1. " ; 2. Antag.; 3. Finger	25	91	83	0	65	100
1. " ; 2. " ; & Fi. simult.	11	0	0	4	0	0
1. " ; & Fi.; 2. Antagonist	7	0	0	0	0	0
1. " ; & Ant.; 2. Finger	0	9	6	0	0	0
1. Antagonist; 2. Protag.; 3. Finger	0	0	11	0	0	0

Two tendencies may be noted from this analysis. First, the difference in order of action of the units under flexion and extension shows less diversity for the latter, second, there is a difference in order of action depending upon the size of load, namely, that under zero load the finger moves prior to the antagonist in the majority of instances, especially in extension movements; whereas under larger loads both antagonists operate before the finger in 85% of the cases.

(iii) Irregularities of time intervals: Comparison of the speed of finger stroke with the latencies between the muscles showed no correlation. This is in contrast with relationships previously indicated in fixation (p. 27) and in pursuit (p. 32).

(c) Qualitative analysis: In movements against load, the angle of contraction made by the antagonistic muscle was steeper in proportion to the size of the load, although the angle by the protagonist was always greater than this. This indicated again that the greater the energy required for a given task, the more intense is the antagonistic action.

One other feature of the ballistic records deserves comment. It is sometimes assumed that in ballistic movements of the fingers, such as in typewriting, piano playing, etc., the protagonist relaxes whilst the finger is *en route*, the excursion being completed presumably by momentum (19). None of our records substantiates this view as far as our subject is concerned. The prime mover, having attained as great a degree of contraction as our markers would indicate remained there throughout the stroke and until the subject voluntarily relaxed. Whether intensive training would permit relaxation of the protagonist in ballistic movements to occur relatively early in the course of the overt movement could readily be investigated by the technique here used.

D. *Oscillatory Movements*

Table V shows the results of the oscillatory movements of 30 degrees, at maximum speed against zero load. For our purpose only the initial movements of the finger and muscles were considered, and the findings agree with those under previously described conditions. Both muscle systems invariably act and always in the direction of contraction.

E. *Involuntary Movement—Extension*

The records of finger extension induced by electrical stimulation reveal a gradation in the time intervals between the action of the muscles. With zero load, if the electrical stimulus was weak (secondary coil 8 cm. or more) no flexor action occurred, although there was mild extensor action with slight finger displacement. With medium intensities (secondary coil from 7.3 to 8 cm) very slight flexor activity was recorded. This antagonistic action was delayed about 200 to 400 sigmata after the protagonist reacted, but preceded the finger movement in 89% of the cases. Stimuli of very

TABLE V

Oscillatory Movements—Zero Load

(1) No.	Finger Speed Averaged Acceleration Degrees per Sigma	No. 1 Unit	Time in Sigmata	No. 2 Unit	Time in Sigmata	No. 3 Unit
	Flexion					
1	.089	F	5	E	31	Fi
2	.086	"	10	"	29	"
3	.085	"	15	"	19	"
4	.074	E	7	F	32	"
5	.067	F	4	E	37	"
	Extension					
1	.077	E	13	Fi	31	F
2	.077	"	17	"	43	"
3	.076	"	24	"	27	"
4	.070	"	26	"	33	"
5	.069	"	26	"	37	"
6	.064	"	19	"	35	"

Showing order of action units and time intervals, in sigmata; during initiation of oscillatory movements. The upper table is for *flexion* movements and the lower for *extension* movements. Both sets of trials against zero loads. F = Flexor; E = Extensor; Fi = Finger.

strong intensity (on secondary coil from 6.5 to 7.2 cm) gave rise to pronounced flexor contraction from 5 to 33 sigmata after the contraction of the extensor.

The effect of increasing the finger load was to reduce the amplitude and velocity of finger movement. In the case of the maximum load (550 gms.) it was not possible to elicit a finger movement even with stimulation of extreme intensity (6.8 cm. on coil), although voluntarily the subject could move such a load.

Qualitative: An objective difference between voluntary and involuntary stimulations of the extensor was in the speed with which the antagonist contracted, the angle for the former being much steeper than for the latter.

V. Conclusions

Conclusions from this study concern the character of initial action of antagonistic muscles during voluntary change from rest to effort; initial action of muscles during voluntary change from effort towards less effort, *i.e.*, relaxation, is not considered. The evidence from finger movement of one adult subject working under conditions of fixation with loads, pursuit, fast uni-directional strokes and fast reciprocating strokes shows that:

1. Both of the antagonistic muscles exhibit activity.
2. In direction, the antagonist invariably *contracts* initially, as well as the protagonist.
3. In time relation, the initial activity of the opposed muscles is not regular. Under the conditions investigated, the antagonist usually succeeds the protagonist, but may coincide with it or occasionally precede it.
4. The latency period between the initial contractive activity of the muscles is affected by numerous factors, including the outer task, *e.g.*, load; the articular function, *e.g.*, direction of limb movement; the intensity of volition, *e.g.*, readiness and degree of effort.
5. In quality of action, the 'angle'' of muscular response is steeper the more intense the voluntary effort; is steeper for the prime mover than for the antagonist; and is steeper for both muscles in voluntary than in non-voluntary response (electrical) giving like finger movement.

Upon this evidence it is concluded that under these conditions antagonistic muscle action is not of the type defined as simple reciprocal innervation, *i.e.*, that the antagonist relaxes at or about the time that the protagonist contracts. Rather that the initial muscular action is of the type, double reciprocal innervation, *i.e.*, that both muscles contract; this action being simultaneously or in succession, but at different rates and amounts, giving overt movement as a resultant.

Further problems concerning the time order and relative rates of muscle contraction for voluntary change from rest to effort and also from effort towards relaxation, remain to be studied. The technique of registration here used would suffice in part for this.

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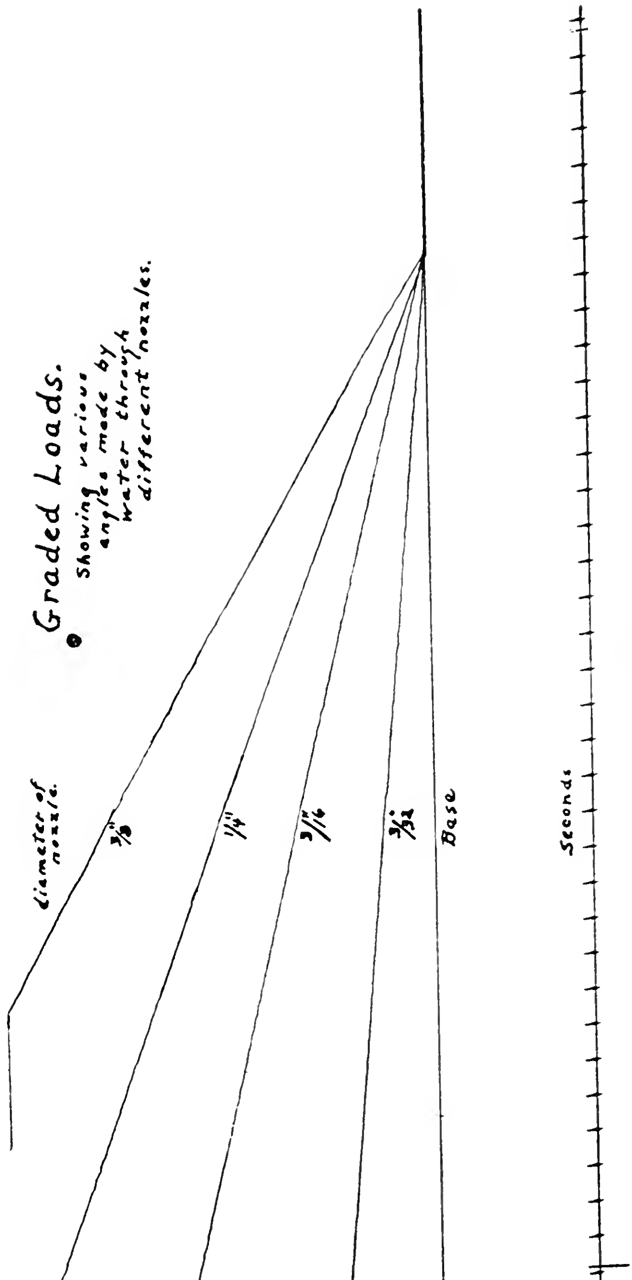

PLATE 2

Showing lines made on smoked paper by pointer indicating gradually increasing loads of various rates depending on size of nozzle used.

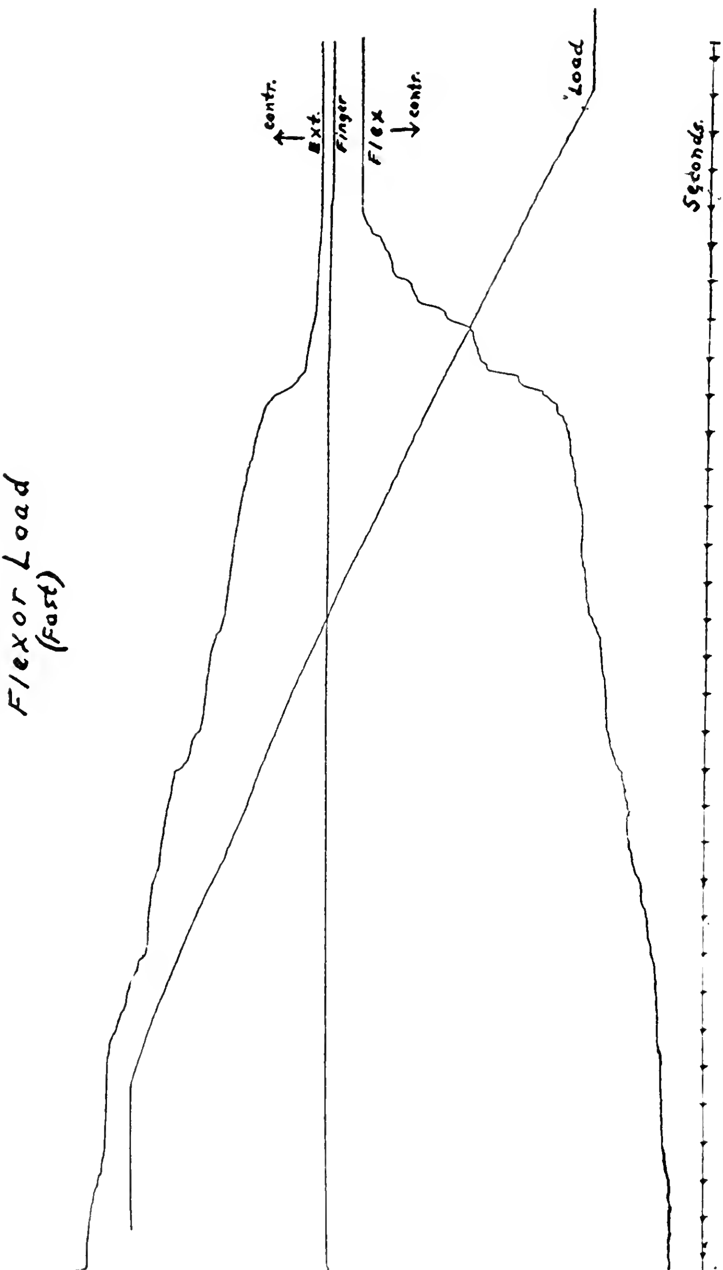

PLATE 2 (*Continued*)

Showing typical record of Voluntary Fixation. Note co-contraction.

PLATE 3

Records of finger movements in pursuit of medium speed taget pointer, showing the accompanying muscle action.

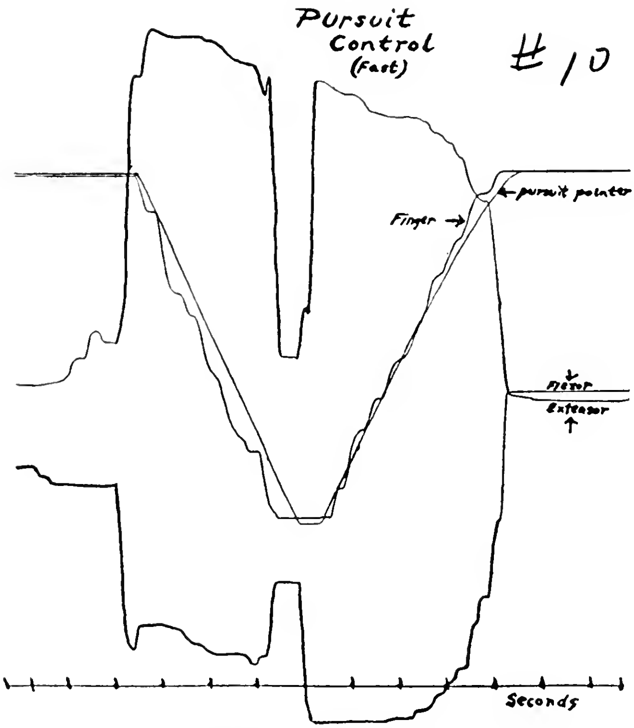

PLATE 3 (*Continued*)

Records of finger movements in pursuit of fast target pointer, showing the accompanying muscle action.

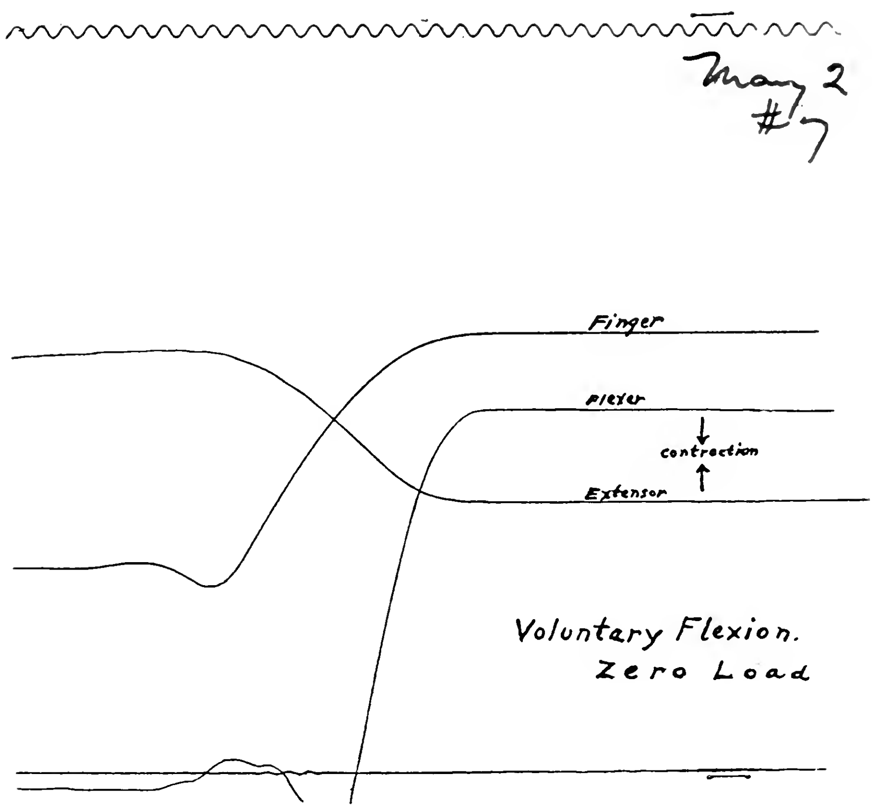

PLATE 4

Record of rapid finger stroke (flexion) showing accompanying muscle action.

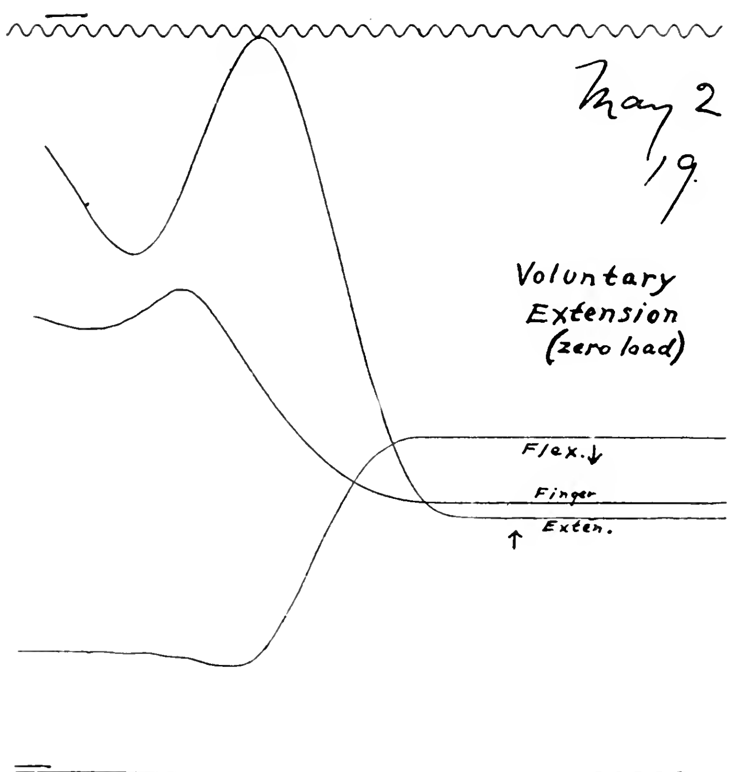

PLATE 4 (*Continued*)

Record of rapid finger stroke (extension) showing accompanying muscle action.

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